PEDALIODES PHERETIAS (HEWITSON) FORM GRISEOLA WEYMER (NYMPHALIDAE: SATYRINAE): ITS IDENTITY AND AVAILABILITY, WITH DESCRIPTION OF A NEW SPECIES

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ABSTRACT. The nominal taxon, *Pedaliodes pheretias* (Hewitson) form *griseola* Weymer, a largely neglected satyrine butterfly from the Andes of southern Colombia, has been recognized in the literature as an infrasubspecific taxon, and the name is not available. Morphological comparisons indicate that this is a distinct species, and it is named *Pedaliodes gustavi*, new species. The geographical range of this species is extended to northern Ecuador. Brief comments concerning closely related taxa are accompanied by formal designations for a neotype of *Pedaliodes chrysotaenia* (Hopffer) form *fassli* Weymer and a lectotype of *Pronophila pheretias* Hewitson.

RESUMEN. El taxón nominal *Pedaliodes pheretias* (Hewitson) forma *griseola* Weymer, un satírido altiandino del sur de Colombia, se ha reconocido en la literatura como un taxón infrasubespecífico, por ello el nombre se considera no disponible. Las comparaciones morfológicas indican que este taxón representa una especie distinta, por lo cual aquí se le denomina *Pedaliodes gustavi*, nueva especie. La distribución geográfica de la misma se extiende hasta el norte de Ecuador. Se hacen breves comentarios concernientes a los taxones cercanamente relacionados con ella y se designa, un neotipo para *Pedaliodes chrysotaenia* (Hopffer) forma *fassli* Weymer y un lectotipo para *Pronophila pheretias* Hewitson.

Additional key words: Colombia, Ecuador, Pedaliodes fassli, Pedaliodes gustavi n. sp., Pedaliodes negreti, Pronophilini.

With 270+ recognized species and subspecies, the Neotropical butterfly genus Pedaliodes Butler (Nymphalidae: Satyrinae) is exceedingly speciose (Viloria 2002). This is significant not only because of its extraordinary diversity, but also due to its unusual biogeography. The distribution of the genus is characterized by highly localized, endemic species, between mountains/ranges and at different elevations in montane tropical America, most remarkably in the northern and central Andes (Adams 1985, Viloria 1998). These features, together with the marked sedentary behavior of its species, most of which are strongly associated with woody bamboos in pristine cloud forest biotopes, render them as potentially good ecological indicators (Adams 1983). In our view, taxonomically reliable measurements of diversity within the genus Pedaliodes, at a general or local geographical scale, may prove to be useful tools for predictive criteria or models to quickly assess the uniqueness of selected areas in the Andean realm. Insects, such as these, are bioindicator species, relatively abundant in the wild, and therefore, not too difficult to study. Although populations of some *Pedaliodes* are rather limited in number or sometimes not easily accessible, they deserve the attention of conservation biologists. Even local or thorough biodiversity surveys cannot be properly completed and make this information available for evolutionary, ecological, or conservation studies without the proper identification of the species present and the resolution of any potential systematic problems. The taxonomy of this genus, currently under revision by the senior author, poses two major, practical limitations: (1) The dependence on traditional morphology for comparative study due to the scarcity of specimens for ontogenetic, genetic, or molecular research. Currently 50% of the taxa are only known either from the original descriptions only, with the types lost, single specimens, or a series of less than 10 specimens, usually quite old. (2) The relative paucity of available characters from wing pattern and genitalia, possibly due to convergence and few clear-cut diagnostic features, found mainly among species that are not necessarily closely related to each other.

During revisionary studies, identification problems have been found in 14 taxa currently associated with *Pedaliodes*, whose types have not yet been located. These currently include: *Pronophila exanima* Erschoff [now *Pedaliodes exanima* (Erschoff)], *Pedaliodes asconia* Thieme, *P. auristriga* Thieme, *P. paeonides* f. *costipunctata* Weymer [now *P. costipunctata* Weymer], *P. chrysotaenia* f. *fassli* Weymer [now *P. fassli* Weymer], *P. pheretias* f. *griseola* Weymer, *P. luperca* Thieme, *P. niphoessa* Thieme, *P. pheres* Thieme, *P. pausia* f. *lucipara* Thieme, *P. simpla* Thieme, *P. pactyes* f. *spina* Weymer [now *P. spina* Weymer], *P. syleus* Thieme, and *P. tucca* Thieme.

Most of these taxa are quite distinct, and their descriptions are either explicit enough or appropriately illustrated. We have examined specimens in several of the major butterfly collections, and most of them can be confidently identified to the specific level. However, there are two critical problems which require attention. The first one refers to *Pronophila exanima* Erschoff, the description and accompanying figure of

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which represent a completely unmarked, dark brown species of *Pedaliodes*. It was described from a single female taken by Konstanty Jelski in Pumamarca (Junín), Peru. According to the author, the specimen was deposited in the museum of the University of Warsaw (Erschoff, 1875:142). However, several efforts have been made to locate it without success (Pyrcz, pers. com.). The case will remain an enigma, until a more rigorous study of the Peruvian *Pedaliodes* is completed. This country contains a very rich fauna with several unmarked species not unlike *P. exanima*.

The second case involves the Colombian *Pedaliodes* pheretias (Hewitson) form griseola Weymer (1912). Gaede (1931) in his catalog considered it as an aberration of P. pheretias. Subsequent authors, who monographed the pronophiline fauna of Colombia following Weymer's work (Krüger 1924, Adams 1986, Pyrcz 1999), completely overlooked it. The single female of this taxon taken by Anton Fassl in the Paso del Quindío was distinguished from that of P. pheretias from the same locality by "having the ground-colour of the entire underside of the hindwing yellowish greybrown, finely striated all over with dark brown, so that the costal and anal spots have almost disappeared" (Weymer 1912:258, in Seitz 1907-1924). The illustration in Weymer (op. cit., pl. 54, row f) is of such poor quality that it is difficult to see any difference with respect to other species of the P. pheretias group. The name has never been applied in a species-group sense, and, as such, is not an available name (Article 45.6.4: International Code of Zoological Nomenclature, 4th edition, [ICZN 1999]).

There has been much confusion associated with the taxonomy of P. pheretias (Figs. 1, 7) and other similar species from Colombia and Ecuador. For example, Fassl (1910:132, 1911:26) and Krüger (1924:31) may have misidentified other taxa, at least in part, under this name. Adams (1986:316-317) thought the occurrence of P. pheretias in the Cordillera Central of Colombia as doubtful, although Pyrcz (1999:364) asserted that it does occur in the mountains of Puracé, along with other related species. We have not seen specimens of P. pheretias from Colombia, but there are records north of Quito, close to the Colombian border, and this species might well range further north into the Cordillera Central of southern Colombia. An alleged sister species of P. pheretias, P. fassli Weymer (Fig. 2), is endemic in the Cordillera Occidental of Colombia, where P. pheretias does not exist (Adams 1986). Another similar species is P. negreti Pyrcz (Figs. 5, 6), which is an endemic in the Cordillera Central, where it must be altitudinally parapatric with P. pheretias.

Two Colombian (both sexes) and five male Ecuado-

rian specimens represented in the collections of the Allyn Museum of Entomology evidently belong to this same group, but these seem to represent another, darker taxon. The female was collected by S. and L. Steinhauser at Fassl's locality "Quindio Pass", and its external characters match well with those described by Weymer for *Pedaliodes pheretias* f. griseola.

A number of observations of wing pattern and male genitalia and comparisons with homologous characters of related taxa (see also discussion below) suggest that this is a separate species, and not merely a subspecies of *P. pheretias*. However, since *griseola* is not an available name, we are describing this taxon as new under a different name.

Abbreviations. AME: Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL, USA; BMNH: The Natural History Museum, London, UK; genit. prep.: genitalic preparation; HC: Hewitson Collection; PUCQ: collection of Pontificia Universidad Catolica, Quito, Ecuador; TL: type locality; TWP: Collection of Tomasz Wilhelm Pyrcz, Warsaw, Poland; WAS: Polish Academy of Sciences, Warsaw, Poland.

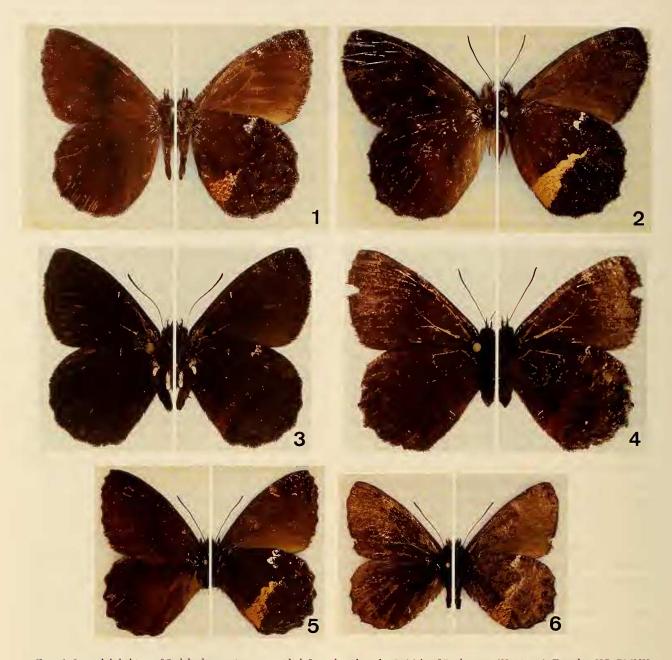
Pedaliodes gustavi Viloria, L. Miller & J. Miller, new species (Figs. 3, 4, 8)

Pedaliodes pheretias (Hewitson) form griseola Weymer, 1912:258, pl. 54, row f.

Pedaliodes pheretias (Hewitson) ab. griseola Weymer; Gaede, 1931:497.

Description. Male (Fig. 3). FWL: 26.6–28.0 mm (27.6 mm on Holotype); mean 27.6 mm; (n = 6). Eyes brown, hairy; palpi erect, brown, with regular brown hairs and longer black hairs, and two and a half times as long as head; antennae, shaft dark orange, club dark brown, gradually formed, and nearly reaching to half costa. Body hairy, dorsally blackish brown with brown hairs; ventrally lighter, especially on legs and abdomen. Upperside: ground color uniform dark coffee brown; fringes with few sparse white scales. Wing upperside with broad androconial patch present on forewing discal area, extending to distal half of discal cell. Underside: ground color of forewing dull dark brown, slightly paler toward tornus; postdiscal-submarginal band faint, only indicated by some pale dusting of white scales near subapical and apical area; hindwing darker brown than forewing with a prominent white midcostal spot very distinct, white dots absent; anal wedge present, but faint and dark chestnut in color.

Female (Fig. 4). FWL: 28.0 mm; (n = 1). Forewing subtriangular, apex softly truncated, outer margin smooth and convex with tornus slightly rounded; hindwing suboval, outer margin moderately scaloped. Wings, upperside ground color warm chocolate brown, slightly lighter towards the distal half; hindwing, notably hairy on basal half and along anal region; some intermixed black and white scales along fringes. Underside ground color as on upperside, but a lighter post-discal-submarginal band on both wings; forewing band speckled with white and (less) dark scales near the costal margin; coffee brown scales forming irregular marbling along the costa and the marginal area, with a series of five (or six), fine, submarginal white dots, within cells, from veins $\rm R_4$ to $\rm Cu_1$ (or $\rm Cu_2$); hindwing, ground color marbled with dark coffee brown, including the lighter band; white scales dusted sparsely over anterior half of wing and marginal area, postdis-



FIGS. 1–6. Adult habitus of *Pedaliodes* species; upperside left, underside right; 1. Male of *P. pheretias* (Hewitson), Ecuador, HC, BMNH type No. Rh. 3986 [Lectotype, herein designated]; 2. Male of *P. fassli* Weymer, Colombia, W. Cordillera, Mte. Socorro, 3800 m, Fassl [Neotype, herein designated, BMNH]; 3. Holotype male of *P. gustavi*, new species, Ecuador: Carchi, Monte Chilles, 3650 m, xii-1973, R. de Lafebre, A. C. Allyn Acc. 1974-7 [AME]; 4. Paratype female, same species, Colombia: Tolima-Quindio, La Linea (Quindio Pass), 3300 m, 21-xi-1974, S. & L. Steinhauser, A. C. Allyn Acc. 1975-17]; 5. Male of *P. negreti* Pyrcz, [Colombia, Cauca, Puracé], Páramo de Neiva, 2800 m, 30-x-1917, [Krüger] [Holotype, data in Pyrcz (1999) appears to be wrong] [WAS]; 6. Female, same species, Colombia, Cauca, P. N. Puracé, Term. San Juan, 3150–3200 m, 28/30-iii-1996, T. Pyrcz [Allotype, TWP].

cal white mark from costa to vein Rs, followed by some white dusting in cell $Rs-M_1$; postdiscal-submarginal white dots in cells $Rs-M_1$ and Cu_1-Cu_2 , respectively; a dark orange suffusion along proximal region of lighter band, resembling an anal wedge extending from the middle of wing but outside the cell to anal angle.

Male genitalia (Fig. 8). Pedaliodes gustavi has a broader and more robust aedeagus than that of P. pheretias, although their degree of contortion are similar. The other major difference between the male genitalia of these two taxa is found in the shape of the

valva: it is distally deeper in *P. pheretias* (Fig. 7), and has a more pronounced apical process. Conversely, the valvae of *P. gustavi* are basally deeper, and their dorsal processes go beyond the extremity of the main apex. Some additional, minor differences can be seen, such as size, shape and orientation of the saccus. Both genitalia also differ from that of *P. negreti* (Pyrcz 1999:376, Fig. 11). From lateral view, the latter has a more incurvated uncus, and a strongly sinuous vinculum. In *P. pheretias* and *P. gustavi*, it is almost straight. The saccus of *P. negreti* is also considerably longer than those of the other two

species. At present the male genitalia of *P. fassli* is unknown as the only specimens known to us (two individuals at the BMNH, recognized as males because of the androconial scales on the forewing) are without abdomens.

Described from seven specimens, six males and one female, from southwestern Colombia and northern Ecuador.

Types. Holotype male: ECUADOR: CARCHI: Monte Chilles, 3650 m, xii-1973, R. de Lafebre; A. C. Allyn Acc. 1974-7 (Allyn Mus. Photo No. 960923/15–16). Paratypes: 1 male, 1 female, COLOMBIA: TOLIMA-QUINDIO: La Línea (Quindio Pass), 3300 m, 21-xi-1974, S. & L. Steinhauser, A. C. Allyn Acc. 1975-17; ECUADOR: 2 males, COTOPAXI: Laguna Los Anteojos, 3950 m, iv-1971, R. de Lafebre, A. C. Allyn Acc. 1971-18; 2 males, data as Holotype.

Disposition. Holotype male, four male and one female paratypes in AME; one male paratype ceded by AME to PUCQ.

Etymology. This species is named in honor of Gustav Weymer who first recognized its distinctness, even though he misinterpreted its taxonomic hierarchy.

Distribution. 3300–3950 m. Known from the southern part of the Cordillera Central of Colombia (Tolima) and the adjacent main ridge of the Andes of Ecuador (Carchi and Cotopaxi).

Evidently, *P. gustavi* is quite rare in collections, but perhaps is less so throughout its natural range. The fact that only seven specimens have been detected among more than 6,000 *Pedaliodes* specimens known from the area in question needs to be interpreted with caution. It could either be a sign of true rarity, or a reflection of the poverty of records for a particularly localized, high altitude taxon.

Associated taxa and type designation. Dealing with the taxonomic solution of the particular problem of *P. gustavi* has also required comparative research of other species of *Pedaliodes*. Based on these investigations in several major butterfly collections in America and Europe, and upon the examination of specimens associated with *Pedaliodes pheretias* and related species, the following types are hereby designated:

Pedaliodes fassli Weymer. (TL: 3400 m, Monte Socorro, Colombia): COLOMBIA: 1 male, W. Cordillera, M[on]te. Socorro, 3800 m, Fassl, NEOTYPE of P. fassli Weymer, herein designated, AB [BMNH] [Red label [printed]: Pedaliodes fassli WEYMER, 1912 / & NEOTYPE / Designated by A. L. Viloria, / L. D. Miller & J.Y. Miller, 2002]. This taxon, proposed by Weymer as a form of P. chrysotaenia (Hopffer), was described in a manner of a geographically separated entity, therefore under the same provision of the "Code", fassli was suggested in a manner that can be interpreted as an available subspecific name.

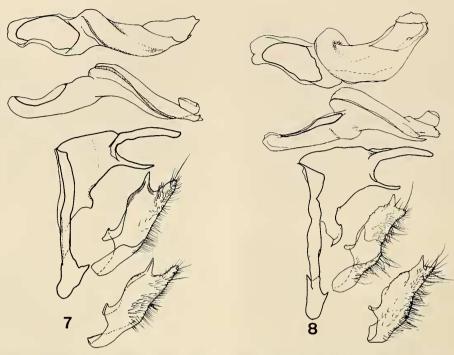
Additional material examined. 1 male, same data as above, 3600 m, vi-'09, (1269A), [BMNH AB].

Pedaliodes pheretias (Hewitson). (TL: Galgalán, Ecuador): ECUADOR: 1 male, Ecuador, HC, BMNH type No. Rh. 3986, Lectotype of Pronophila pheretias Hewitson, herein designated [BMNH] [Red label [hand-written]: Pronophila pheretias HEWITSON, 1872 / ♂ [printed]: Lectotype designated by/ A. L. Viloria, 1997]. This specimen is in the W. C. Hewitson collection, deposited in the collections of the Natural History Museum in London. It represents the only individual available to that author to illustrate the original description of P. pheretias (Hewitson, 1872: pl. [28], fig. 46).

Additional material examined. 1 male, Rio Pastaza, vii-[19]34, Brit. Mus. 1969-293; 1 male, Provincia de Pichinda [sic], SW. of Quito, above Chiriboga, 2950-3000 m, 31-vii-1986, M. J. & J. Adams, A/A; 1 male, same data, 3150 m, 29-viii-1986; 1 male, Provincia de Napo, E. below Papallacta, 2800 m, 29-viii-1986, M. J. & J. Adams, A/A; 1 male, old Sto. Domingo rd., 9.8 km W. of San Juan, N. Quito, 0°18'S, 78°42'W, 2790 m, road side primary forest, temp. zone, 15-ix-1974, R. Bristow, (genit. prep. ALV213-96), RB1; 1 male, old Sto. Domingo rd., 6.6 km W. of San Juan, N. Quito, 0°18'S, 78°39'W, 3010 m, road side primary forest temp. zone, 15-ix-1974, R. Bristow, RB1; 1 [male], km 39 W. of Limón, 2°58'S, 78°39'W, 2740 m, temp. forest, 29-iii-1975, R. Bristow, RB2 [BMNH]; 1 male, Zamora-Chinchipe, Cajanuma, 2700-2800 m, 10-xi-1996, A. Neild [TWP].

Pedaliodes pheretias (Hewitson) form griseola Weymer. It has been disposed of above under Pedaliodes gustavi, new species.

Material examined of *Pedaliodes negreti* Pyrcz. (TL: Páramo de Neiva, 2800 m, [Puracé], Colombia): COLOMBIA: 2 males, Cauca, Puracé Ntl. Pk., param[o] del Buey, 3000 m, 10-iii-1976, S. & L. Steinhauser, A. C. Allyn Acc. 1976-9 [AME]; 1 male, P. N. Puracé, Term. San Juan, 3150–3200 m, 28/30-iii-1996, T. Pyrcz; 1 female, same data (Fig. 6);1 male, Cauca Prov., Páramo Malvasá, 3200–3400 m, 17/23-ii-1997, T. Pyrcz, [allotype and paratypes of *P. negreti* Pyrcz] [TWP]; 1 male, Páramo de Neiva, 2800 m, [Puracé], 30-x-1917, [Krüger], [holotype *P. negreti* Pyrcz; data on the holotype disagree with the published information by Pyrcz] (Fig. 5) [WAS]; ECUADOR: 1 male, Cotopaxi, Milimbanco, 4090 m, xi-1970, R. de Lafebre, A. C. Allyn Acc. 1971-7; 1 male, Cotopaxi, Laguna de Los Anteojos, 3950 m, iv-1971, R. de Lafebre, A. C. Allyn Acc. 1971-18; 1 male Imbabura, Cordillera Cotacachi, 3750 m, xi-1971, R. de Lafebre, A. C. Allyn Acc. 1972-6; 1 male, Carchi, Monte Chilles, 3650 m, xii-1973, R. de Lafebre [AME].



FIGS. 7, 8. Male genitalia of two closely related parapatric species of *Pedaliodes*; valvae and aedeagi have been removed from their original position; the latter shown in dorsal (above) and lateral (below) views. The same magnification has been used in each drawing: **7.** *P. pheretias* (Hewitson); **8.** *P. gustavi*, new species.

DISCUSSION AND CONCLUSIONS

The recent recognition of a taxon that had been neglected by entomologists for about 70 years required the consideration of three main questions, one hierarchical (is it a species or a subspecies?), one nomenclatural (what name should we apply to it?) and one of typification (which are the types and where are they?). The treatment given to these issues is discussed separately:

Hierarchy. Our criteria to determine species or subspecies within the genus *Pedaliodes* are the result of a balanced combination of what we observe in morphology and biogeographic patterns. Different subspecies are always allopatric (by definition). They differ in wing color pattern, but have almost identical genitalic structures. On the other hand, different species may be sympatric, parapatric or allopatric. They usually differ considerably from each other in wing patterns, but there are few difficult instances in which it is not evident, especially among darker and unmarked taxa. In such cases, the pattern and extent of the androconial patches on male forewing has been comparatively studied to separate different species (Pyrcz & Viloria 1999). Both wing and androconial patterns are external characters easy to interpret by nonspecialists. However, determination of stable differences in male genitalia is our definitive criterion used to distinguish *Pedaliodes* species.

The wing pattern of *P. gustavi* is sufficiently distinct from those of its closest relatives (compare Figs. 1–6); its male genitalia, as compared in the relevant section of the description above, is distinct enough as to warrant its own specific status (Figs. 7, 8). Additionally, there are ecological and biogeographic evidences to support our claim that *P. gustavi* is a separate species in the 'pheretias-group.' Pedaliodes pheretias (2700–3150 m), P. gustavi (3300–3900 m), and P. negreti (2800–4090 m) occupy different altitudinal belts in the southern mountains of the Cordillera Central of Colombia and the adjacent Andes of Ecuador. They are either parapatric or partly sympatric (allelopatric sensu Papavero et al. 1994), which according to the model of speciation proposed by Adams (1985) preclude the possibility of being conspecific. Perhaps they may not even be sister species. In any case, the putative sister species of *P. gustavi* should be its allopatric, yet ecological equivalent, P. fassli, which flies in the Cordillera Occidental between 3400 and 3800 m.

Nomenclature. We were tempted to redescribe this taxon under the Weymer name, but as explained in the introductory notes above, *P. griseola* is not an available name. Therefore, the decision was made to describe it under an entirely new name.

Typification. The original description by Weymer does not mention the disposition of the female type specimen of *Pedaliodes pheretias* f. *griseola*. Its collec-

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tor, A. H. Fassl, was also a dealer, and probably sent several South American satyrines directly to Weymer for study. Four types of the ten taxa originally described by Weymer under 'Pedaliodes' are in the ZMHB (P. albopunctata Weymer 1890, P. phaedra (Hewitson) f. melaleuca Weymer 1890, P. reissi Weymer 1890, and P. uniformis Weymer 1912). The remaining six (all collected by Fassl in Colombia) include P. chrysotaenia (Hopffer) f. fassli Weymer 1912, P. pactyes (Hewitson) f. spina Weymer 1912, P. paeonides (Hewitson) f. costipunctata Weymer 1912, P. pausia (Hewitson) f. lucipara Weymer 1912, P. pheretias (Hewitson) f. griseola Weymer 1912, and P. tomentosa Weymer, 1912, have not yet been located. According to Horn & Kahle (1935:301), Weymer's collection was deposited at the Humboldt University Museum in Berlin. It was located on the fifth floor, which was unfortunately partially destroyed by a bomb during World War II. We believe that the missing types were lost at that time, and neotypes have been designated above to objectively define the taxa under consideration. According to G. Lamas (pers. com.), there still is the possibility that some butterfly specimens studied by Weymer might have been returned to Fassl. Should this have happened, the true types could have survived either in private or public collections elsewhere as Fassl's material is scattered all over the world.

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LITERATURE CITED

ADAMS, M. J. 1983. Andean brown butterflies, pp. 473–476. *In* Wells, S. M., R. M. Pyle & N. M. Collins (eds.), The 1UCN invertebrate red data book. IUCN, Gland.

- ——. 1985. Speciation in the pronophiline butterflies (Satyridae) of the northern Andes. J. Res. Lepid. 1985 (suppl. 1):33—49.
- ——. 1986. Pronophiline butterflies (Satyridae) of the three Andean Cordilleras of Colombia. Zool. J. Linn. Soc. 87:235–320.
- ERSCHOFF, N. 1875. [Description of new exotic Lepidoptera]. [Trudy russk. ent. Obshch.] 8(2):140–149, pl. 3. [in Russian].
- FASSL, A. H. 1910. Tropische Reisen. II. Ueber den Quindiupass. Ent. Z. 24:113–114, 118, 127–128, 132–133, 137–138, 142–144, 149–150.
- 1911. Die vertikale Verbreitung der Lepidopteren in der Columbischen Central-Cordillere. Fauna Exot. 7:25–26.
- GAEDE, M. 1931. Satyridae. II. In Strand, E. (ed.), Lepidopterorum Catalogus. 29(46):321–544.
- HEWITSON, W. C. 1872. Satyridae. Pronophila VII. Illustrations of new species of exotic butterflies, 5. John van Voorst, London. Pp. [51–52], pl. [28].
- HORN, W. H. R. & 1. KAHLE. 1935–1937. Über entomologische Sammlungen. (Ein Beitrag zur Geschichte der Entomo-Museologie). Ent. Beih. Berl.-Dahlem 2:1–160 + 12 pp., pls. 1–16; 3:161–296, pls. 17–26; 4: 297–536 + [iv], pls. 27–38.
- ICZN [INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE]. 1999. International code of Zoological Nomenclature. 4th ed. The International Trust for Zoological Nomenclature, London. xxx + 306 pp.
- London. xxx + 306 pp. Krüger, E. 1924. Beiträge zur Kenntnis der columbischen Satyriden. Ent. Runds. 41:23–24, 27–28, 31–32, 35.
- Papavero, N.; J. Llorente-Bousquets & J. Minoro-Abe. 1994. Formal definitions of some new biological and geological terms for use in biogeography. Biogeographica 70:193–203.
- PYRCZ, T. W. 1999. The Krüger collection of pronophiline butterflies. Part II: Genera Manerebia to Thiemeia (Lepidoptera: Nymphalidae: Satyrinae). Lambillionea 99:351–376.
- PYRCZ, T. W. & A. L. VILORIA. 1999. Mariposas de la tribu Pronophilini (Nymphalidae, Satyrinae) de la Reserva Forestal Tambito, Cordillera Occidental, Colombia. 1ra. Parte. Convergencia de los patrones de coloración en mariposas andinas: siete nuevas especies del género *Pedaliodes* Butler. SHILAP, Revta. Lepid. 27:173–187.
- VILORIA, A. L. 1998. Studies on the systematics and biogeography of some montane satyrid butterflies (Lepidoptera). King's College London / The Natural History Museum, London. 493 pp. [Doctoral Thesis].
- 2002. Limitaciones que ofrecen distintas interpretaciones taxonómicas y biogeográficas al inventario de lepidópteros hiperdiversos de las montañas neotropicales y a sus posibles aplicaciones, pp. 173–190. In Costa, C., S. A. Vanin, J. M. Lobo & A. Melic (eds.), Proyecto de Red Iberoamericana de Biogeografía y Entomología Sistemática PrIBES 2002. m3m-Monografías Tercer Milenio. Vol. 2. Sociedad Entomológica Aragonesa, CYTED, Zaragoza.

WEYMER, G. 1912. 4 Familie: Satyridae, pp. 173–283. In Seitz, A. (ed.), Die Gross-Schmetterlinge der Erde, 2; Exotische Fauna, 5. A. Kernen, Stuttgart.

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